Deep Sea Frontiers: Aid In Preparing a Book MS for Publication

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LONG-TERM GOALS

Identify major current progress in deep sea biology. Define ways of applying new advance in molecular, developmental and evolutionary biology to solving problems in biological oceanography. Finish an illustrated book MS that presents these results for the non-specialist reader.

OBJECTIVES

Organize and interpret the massive bibliography relevant to the above goals. Publish a detailed broad technical essay on this ongoing process (part 2 of 3 was published in August '01 in the J. Exp. Zoology 239:130-168).

APPROACH

Literature search and analysis using mainly the Kline Science Library and other Yale biological information sources. A part time bibliographic assistant is collaborating on this endeavor.

WORK COMPLETED

The book MS has not yet been completed and will no doubt take another years work after this grant period. The journal article just cited was published this year as part of a larger effort (including the deep sea project) not currently aided by ONR.

RESULTS

Probably the best way to demonstrate these is to briefly characterize several of the most stimulating areas of deep sea biological research.

Invading the Deep Sea

Several of the globe's extreme ecosystems, including the deep sea, as well as the polar regions, high mountains and deserts, overwhelm the capacity of almost all animals to flourish there. Typically only a few remarkably rugged types can survive if faced with close to intolerably high or low temperatures, strict scarcity of water, high hydrostatic pressures, minimal oxygen partial pressures and near starvation. Such extremophiles must have been either pre-adapted somehow to the stresses encountered or were capable of adapting effectively to such hardships. The deep sea fauna evolved from shallow water pelagic and littoral animals including types from most of the major marine phyla and many of their constituent taxa.

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These immigrants expanded into the huge volume of by far the largest of the planet's potential ecosystems. Obviously, the time scale for deep sea animal evolution is immensely long. Yet the geological evidence for deep sea biological history is sparse. This is in part due to the continual rather rapid turnover of the sea floor. Steady subduction of the ocean crust occurs at the continental margins and corresponding magma renewal occurs at the mid ocean ridges followed by lateral spreading. Littoral and continental shelf faunas may be richly represented as fossils, but pelagic, oceanic and deepwater preservation is relatively rare.

Paleo Oceanography

Deep oceans are believed to have been present on earth since long before there were any metazoans to inhabit them. Dating to 1000-540 million years ago in the later part of the Proterozoic, documented evidence indicates that world wide geological and climatic changes took place (Hyde, et al., 2000). Independent evidence for a "snow ball earth" during parts of this stressful period may support the presence of a narrow bottleneck for the survival of the then emerging metazoans (Hoffman and Schrag, 2000, Kerr, 2000). Two severe ice ages appear to have occurred just before and about the same time that the first known substantial metazoan fossils appeared in ancient marine rocks. Air temperatures of -50° C presumably prevailed for 10 million years or more.

Under such conditions global primary productivity, obviously, would have been sharply reduced. Also, if the ocean were completely frozen over, the critical sources of oxygenated deep water would be blocked by the thickly frozen upper layers of the seas. As a result, the remaining liquid ocean would likely be lethally anoxic to metazoans. During this kind of severe and prolonged worldwide ice age, all animal life would surely have been forced to the brink of survival. Yet we do know that prokaryotes, algae and protoctists have persisted until the present from their origins perhaps a billion years before these late Proterozoic ice ages.

Deep sea light

Characteristic stresses of the deep sea, defined as depths beyond the edge of the continental shelf, nominally at about 200 m, are increasingly low levels of sunlight absorbed and scattered by the water column. As a result little or no photosynthetic productivity can occur in the deep sea and that little only at its shallowest depths. In turn this means that most deep sea animals down to the deepest abysses depend on that productivity mostly in the top 40 m to 100 m near the surface. For vision the situation is less acute since thresholds can be remarkably low but limited to the upper 800 m to 1200 m for sunlight. Large eyes of undemonstrated function are present in macrourids and some Atlantic Ridge deep sea shrimps, for example, at far greater depths than the limits of sunlight.

Moderate range horizontal migration is also important in food finding by free-swimming near-bottom deep sea macrourids. As scavengers, they depend for their nourishment mainly on discrete food falls, such as fish carcasses that reach the bottom from upper levels of the sea. To find this random, but crucial, manna, they must actively and effectively search large suitable areas. Also down at least to bathypelagic depths bioluminescence and vision show remarkably varied types of co-adaptation.

High Hydrostatic Pressure

Undoubtedly the signature stress of the deep sea stem from its particularly *high hydrostatic pressures* at depth (Macdonald, '75). Yet we usually think of animal physiological chemistry as functioning at about one atmosphere pressure. Ordinarily in the laboratory or clinic at sea level, the thermodynamic p delta V element of the reaction kinetics is ignored because its contribution is nearly zero. But if metabolic reactants and products have different volumes, this factor becomes sensitive to pressure change and shifts the rate, equilibrium point and possibly even the direction of a given biochemical reaction.

Both gene and enzyme activities typically involve volume changes and hence their metabolic reactions can also be highly sensitive to pressure. Also in living membranes high pressures disturb the basic two-layered lipid structure essential to many normal cellular functions. At the molecular level, particular components, such as hormones and neural transmitters, that are key integrating elements, are often sensitive to pressure. For instance, certain G-protein coupled signal transduction systems are affected by pressure as are many enzymes. In two closely related deep sea fish species, for example, the binding properties of a relevant G-protein in brain cell membranes were proved to be "tuned" to the different depths of their habitats, about 400 m for one and between 600 m and 1000 m for the other. Pressure may also influence certain structural details of nucleic acids and other essential large molecules.

To avoid such an unfavorable or even fatal imbalance on entering a deep sea habitat, any shallow water animal must either be immune to such influences or modify its biochemical systems to minimize any pressure impact, even though some efficiency in energy use may thereby be lost. Certain groups such as the ophiuroids seem facile in functioning in deep water. Nearly a quarter of their 2000 species live at depths greater than 1000 m. by mechanisms still unknown (Hendler and Tran, 2001).

But some deep sea fishes, in addition to evolving enzymes that are less pressure sensitive, have also increased the concentrations of trimethylamine oxide in various tissues. This reduces pressure's effect of slowing enzyme function (Yancey, et al., 2001). Substantial linear increases in the natural tissue concentrations of trimethylamine oxide were found between species living at increasing depths from shallow, to bathyal and abyssal. The activities of the three enzymes tested in each were normalized in this way in vivo for the depths of their habitats.

Interestingly, some deep sea bacteria can become acclimated to living at different ambient pressures. A protein inventory of *Thermococcus hydrophilus*, a deep sea hyperthermophile, showed that a heat shock-like stress protein was synthesized when they were cultured at low hydrostatic pressures, presumably stressful to them (Marteinsson, et al., '99). Whether, in contrast, shallow water microbes, as well as animals more generally living at great depths make use of such a protective protein remains an important open question.

Deep sea Divers

Remarkably, many kinds of air breathing animals dive aerobically, repeatedly and rapidly down to several hundred meters or more without, as far as we know, suffering from either rapture of the deep or the bends. Record depths for the sperm whale (3000 m.) and male northern elephant seal (1430 m.) are astonishing (Berta and Sumich, '99). However, unlike scuba divers, all of such animal divers hold their breath underwater as long as two hours reported for the sperm whale and female southern elephant seal. Yet with their lungs collapsed and no significant air space within their bodies they avoid the damaging effects of nitrogen gas under pressure.

Also, these marine animal divers must completely refresh their aerobic respiratory system during brief intervals at the sea surface. Critical here are their effective tank capacities for oxygen storage and ways of minimizing the deleterious effects of accumulating carbon dioxide and lactic acid in long animal dives. For deep diving, respiratory gas storage in the gas phase obviously will not do, but binding oxygen to muscle myoglobin is an effective way of storing it.

Diving birds and mammal often have 10 to 30 times the myoglobin in their skeletal muscles as comparable non-diving types (Noren and Williams, 2000). Also, deep diving marine mammals have substantially increased blood volumes and hematocrits that account for half or more of their total stored oxygen (Berta and Sumich, '99). Large size, as in odontocete whales, increases the muscle mass available for oxygen storage and at the same time reduces the mass specific metabolic rate. Both effects, no doubt, contribute to the sperm whales' remarkable diving prowess (Noren and Williams, 2000).

Note, too, that some large fish such as big eye tuna and certain sharks can dive regularly as deep as 500 m. into the sea to pursue vertically migrating prey during the day. Presumably they can swim from warm surface water through several hundred meters of cold deeper water because they have special internal heaters that warm their swimming muscles, brain or eyes and so maintain their high level of metabolism. Big eye tuna also have blood with enhanced oxygen affinity that reduces the stress of low oxygen partial pressures common below 100 m or 200 m. in the open ocean (Lowe, et al., 2000). Whether or not general resistance to rapid pressure change is also involved remains unknown.

- More generally, stress resistance basically is interrelated with metabolic rate, size, longevity, aging, hibernation and diapause as well as corresponding signal receptors and effector mechanisms.

- Evolution is a paradoxical combination of stasis and change. Despite overall evolutionary increases in size, complexity and diversity, small simple and undiversified organisms still flourish after at least two to three billion years of persistence.

IMPACT

The intended future impact of this project is to inform and stimulate the non-specialist reader

about the world's largest ecosystem. As the globe's least accessible one it severely challenges our efforts to understand its far-reaching importance both practically and scientifically.